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The relative controls on forest fires and fuel source fluctuations in the Holocene deciduous forests of southern Wisconsin, USA

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Abstract

Reconstructing fire regimes and fuel characteristics is an important aspect of understanding past forest ecosystem processes. Fuel sources and fire regimes in the upper Midwestern United States have been shown to be sensitive to regional climatic variability such as drought periods on millennial timescales. Yet, records documenting the connections between disturbance activity and the corresponding fuel source fluctuations in mesic deciduous forests and prairie/oak savanna in this region are limited. Thus, it has been difficult to provide a framework to evaluate changes in moisture availability on fire activity and the relationships with fuel source fluctuations in this region. We present high-resolution charcoal analyses of lake sediments from four sites in southeastern-southcentral Wisconsin (USA) to characterize fire activity and fuel source fluctuation in mesic deciduous forests and prairie/oak savanna over the last 10,000 years. We found that fire occurrence across the four study sites has been asynchronous throughout the Holocene, because of site-specific differences that have strongly influenced local fire regimes. Additionally, we found that during periods of high fire activity the primary fuels were from arboreal sources, and during periods of low fire activity the primary fuels were from non-arboreal sources. However, fluctuations in fuel sources did not always correspond to changes in vegetation, or changes in fire frequency.

Keywords: Fire, Vegetation, Fuels, Moisture, Midwest

Introduction

Wildfires are a common and widespread phenomenon that are the result of the interactions between climate (e.g. precipitation and temperature), vegetation (e.g. fuel availability and fuel condition) and ignition (lightning or human) (Whitlock and Larsen 2001). Teasing apart the effects of these variables on fire regimes can be challenging because of variations in the strength of each component over time and space. In addition, how combinations of factors contribute to periods of extreme fire conditions, such as the recent fires in the western United States (Marlon *et al.,* 2012) or Alaskan tundra (Hu *et al.,* 2010; Mack *et al.,* 2011) is not well understood. Knowledge of these complex interactions and more specifically how fire regimes are altered as vegetation changed, can provide greater insight into possible responses to future climate changes.

Moisture availability has direct effects on fire regimes over multiple timescales ranging from years to millennia (Renkin and Despain, 1992). Possible mechanisms for the influence of moisture on fire regime include: i) controlling the incidence of ignitions, ii) determining the likelihood that fires will spread, and iii) changing vegetation type and productivity, and hence the available fuel load (Booth *et al.,* 2006; Podur and Wotton, 2010; Power *et al., 2008)*. Moisture level in fuels is the major factor that determines how readily and how much of the fuel will burn. Thus, moisture availability influences fuel availability. However, there is a complex threshold that exists between very high and very low levels of moisture, such that changes in moisture availability may have unexpected and unpredictable effects on fire regimes depending on the initial climate conditions and further feedbacks with vegetation type (Staver *et al.,* 2011). Increasing moisture availability (i.e. increasing mean annual precipitation, MAP) has been shown to increase fire frequency because of increases in primary productivity, biomass, and fuel load (Krawchuk *et al.,* 2009). This mechanism of increased moisture providing increased fuel availability may also be operating on millennial timescales, at least in grassland systems (Grimm *et al.,* 2011). However, in wetter climates, increased moisture has been shown to decrease fire frequency due to lower ignitions and less-flammable fuel conditions (Krawchuk *et al.,* 2009). Distinguishing these two opposite scenarios within a paleoecological record would be valuable when trying to understand the complex dynamics of past fire regimes.

The climate driven historical movements of vegetation boundaries throughout the upper Midwest have had effects on the fuels for regional fires over millennial timescales (Clark *et al.,* 2001). The prairie/forest boundary is a well-documented vegetation boundary located in the upper Midwestern U.S., which is characterized by an east-west moisture gradient that has fluctuated over time (Baker *et al.,* 1992; McAndrews, 1964; Webb, 1987). The driver for the longitudinal movement of the prairie/forest boundary, and the changes in vegetation from prairie/savanna to mesic deciduous forest, have been attributed to shifts in air mass distribution over time (Bartlein *et al.,* 1984; Nelson and Hu, 2008). However, fire has also been suggested as a factor on vegetation change (Umbanhowar *et al.,* 2011). A previous study in this region noted that mesic deciduous forest composition was not influenced by changes in fire regimes (Long *et al.* 2011). However, it is unknown if this response was consistent across the prairie/forest boundary. In addition, millennial-scale fire histories from prairie/oak savanna ecosystems are sparse in North America (Marlon *et al.* 2009) and baseline information is needed to aid in evaluating the impact of future climate conditions on these ecosystems (Long *et al.* 2011).

To assess the relative roles of climate and fire in the long-term vegetation composition of upper Midwest, fire and vegetation histories were examined from an east-west transect that included two sites in the moist deciduous forests of eastern Wisconsin (Long *et al.* 2011) and two new sites in the drier prairie/oak savanna of central Wisconsin. We hypothesize the following: 1) Long-term regional changes in moisture affected the two sets of sites differently, with the wet locations exhibiting more fire activity as moisture availability decreased and the dry locations showing less response in fire activity with increasing and decreasing moisture conditions, 2) Wet and dry sites showed an increase in arboreal fuel sources as fire activity increased, and 3) Vegetation composition at all sites was dynamic but was not the main factor in limiting fire activity.

Site Description

The four study sites were located in southern Wisconsin: Butler Lake, Lake Seven, Comstock Lake and Lake George (Fig. 1). Butler Lake and Lake Seven are located in the eastern mesic deciduous forest zone, classed in this study as wet sites; and Comstock Lake and Lake George are located in the western prairie/oak savanna zone, classed in this study as dry sites. All sites are kettle lakes with simple bathymetry, small watersheds, and no inflowing or outflowing perennial streams. Butler Lake is 3 ha in size, with a maximum depth of 4 m and a watershed of 200 ha. Lake Seven, which is 5 km south of Butler Lake, is 10 ha in size, with a maximum depth of 7 m, a watershed of 80 ha and is surrounded by large marshlands. Both lakes lie within the moraine deposits of the Green Bay Lobe in eastern Wisconsin, now the Kettle Moraine State Forest. Dominant vegetation includes *Acer saccharum*, *Tilia americana*, *Quercus* spp., with some *Ulmus* spp., *Carya* spp., *Fraxinus* spp., and *Betula papyrifera.* Comstock Lake is 10 ha in size, with a maximum depth of 9 m and a watershed of 50 ha. Lake George, located 60 km to the south of Comstock Lake, is 15 ha in size, with a maximum depth of 7 m and a watershed of 60 ha. Both are located on the outwash plain of the Green Bay Lobe in south central Wisconsin (Fig. 1). Dominant vegetation at these sites includes *Quercus alba*, *Quercus macrocarpa*, *Quercus velutina*, and various prairie grasses and forbs. The study-area climate can be characterized as having warm, moist summers and cool, dry winters. January and July mean monthly temperatures average -10 and 21°C respectively. The wet sites, Butler Lake and Lake Seven, average 600 mm of precipitation annually, while the dry sites, Comstock Lake and Lake George, average approximately 450 mm of precipitation with the majority of the precipitation at all sites falling between April and October. The fire season in this area occurs in spring, prior to summer rains arriving, as temperatures rise and snowmelt occurs (Wisconsin Department of Natural Resources).

Methods

The Butler Lake pollen and charcoal records and the Lake Seven charcoal record used in this study were reported by Long *et al.* (2011). The methods for the new records from

Comstock Lake and Lake George discussed below follow those of Long *et al.* (2011). The analysis of charcoal morphology from Butler Lake and Lake Seven is new to this study. Sediment cores were collected from the deepest part of each lake using a 5-cm diameter modified piston sampler (Wright, 1967). Cores were extruded in the field, wrapped in cellophane wrap and aluminum foil, and then transported back to the laboratory where they were refrigerated and stored. In the laboratory, the core sections were sliced lengthwise, described, and subsampled for charcoal analysis. Subsamples were taken for pollen analysis from Comstock Lake. The chronology for each record was based on ^{14}C dates from terrestrial macrofossils, charcoal and sediment.

Pollen

Sediment samples of 1 cm^3 were taken every 10-40 cm for pollen extraction from Comstock Lake core and processed following (Faegri, 1989). Samples had a known concentration of microspheres added to allow pollen percentages to be calculated and pollen was identified at 400X magnification. A minimum of 300 fossil terrestrial pollen grains were analyzed in each sample. The percentages of each pollen type were calculated relative to the terrestrial pollen sum of the sample.

Charcoal and fire history reconstruction

Charcoal sampling methods for charcoal followed (Long *et al.,* 1998). Sediment subsamples of 2–3 cc were taken at contiguous 1-cm intervals and soaked in 10% solution of hydrogen peroxide for 48-72 hours. The samples were washed through 250 and 125 µm nested sieves. The sieved samples were examined at 25-75× magnification, and all charcoal pieces greater than 125 µm were counted and categorized according to morphology (see description below) (Jensen *et al.* 2007).

Charcoal counts for each sample were converted to concentration (pieces cm^{-2}) and, using the sediment deposition rate, to charcoal accumulation rates (CHAR; pieces cm^{-2} yr^{-1}) at constant time stages to minimize any variations in the record due to fluctuations in the deposition rates. The CHAR records were then decomposed into background and peak components using the model Char Analysis (Higuera *et al.,* 2009). Background charcoal is the slowly-varying trend in CHAR as a primary result of changes in fuel abundance and composition. Peaks, which are positive deviations from the background CHAR (BCHAR), represent input of charcoal as a result of a fire episode (Long *et al.,* 1998). The BCHAR component was then determined using a LOWESS smoother robust to outliers with a 500-year window width. The background values for each time interval were then subtracted from the total CHAR accumulation for each interval. Peaks in the charcoal record (i.e. intervals with CHAR values above background) were tested for significance using a Gaussian distribution, where peak CHAR values that exceeded the 95th percentile are then considered statistically significant (i.e. not the result of natural signal noise or analytical error). This procedure was performed on every 500-year overlapping portion of the CHAR record, producing a unique threshold for each sample. Once identified, all peaks were then screened to eliminate those that resulted from statistically insignificant variations in CHAR (Gavin *et al.*, 2006). If the maximum count in a CHAR peak had a >5% chance of coming from the same Poisson-distribution population as the minimum charcoal count with the proceeding 75 years, then the peak was rejected (Higuera *et al.,* 2009).

Testing for synchronicity in the fire records

We also tested for synchrony in fire event occurrence between Butler Lake and Lake Seven (the paired wet locations) and Comstock Lake and Lake George (the paired dry locations) (Gavin *et al.,* 2006). The K1D analysis computes the multivariate Ripley K-function simplified for one dimension (time steps). K1D computes the dependence between two or more events at a range of time windows.

Charcoal morphology classification

Grasses, forbs, conifer wood, and leaves of many broadleaved tree taxa all produce characteristically distinct charcoal pieces that are preserved in lake sediments (Jensen *et al.,* 2007). All four charcoal records had charcoal pieces identified by the morphology described below. Arboreal charcoal was characterized by three morphotypes: (1) Dark (opaque, thick, solid, geometric in shape, some luster, and straight edges), (2) Lattice (cross-hatched forming rectangular ladder like structure, and with spaces between), and

(3) Branched (dendroidal, generally cylindrical with successively smaller jutting arms). Non-Arboreal charcoal was characterized by two morphotypes: (1) Cellular "graminoid" (thin rectangular pieces; one cell layer thick with pores and visible vessels, and cell wall separations,) and (2) Fibrous (collections or bundles of thin filamentous charcoal that is clumped together) (Jensen *et al.,* 2007; Tweiten *et al.,* 2009).

Charcoal pieces were grouped into non-arboreal and arboreal categories based on their morphology, which allowed for characterization of fuel sources in the charcoal record. This level of detail provides a more precise characterization of past fire regimes than charcoal counts alone. For example, low-intensity surface fire episodes will generally produce a higher abundance of grass/shrub (non-arboreal) charcoal pieces, while major crown fire episodes will produce significantly more hardwood/pine (arboreal) charcoal pieces (Enache and Cumming, 2009). Thus, an abundance of grass/shrub charcoal in a sedimentary interval represents a period in time when non-arboreal fuels were among the primary fuel sources that may represent low-intensity ground fires. Similarly, a sedimentary interval with an abundance of hardwood/pine charcoal represents a period in time when arboreal fuels were the primary fuel sources and the fire regime may have consisted of stand-replacing crown fires.

Results

Sediment cores of 9.19 m and 8.74 m were collected from Comstock Lake and Lake George respectively. The cores can be characterized as consisting of fine-detritus gyttja with basal sediments of sand and silty clay. The chronology for each record was based on ^{14}C dates from terrestrial macrofossils and sediment (Table 1). All dates were converted to calibrated years before present (cal a BP) based on CALIB 6.0.1 (Reimer *et al.,* 2009). The age-depth relations for each sediment record were based on linear interpolation between dates and gave a basal date of 16,600 cal a BP for Comstock Lake and 12,990 cal a BP for Lake George. (Fig. 2).

The pollen percentage data from Comstock Lake, in comparison with other regional vegetation reconstructions, confirms the regional vegetation transitions that occurred over the last 16,000 years (Williams *et al.,* 2009). Prior to 14,700 cal a BP the Comstock Lake landscape was dominated by *Picea* forests before transitioning to *Pinus/Ulmus* forests and then to *Quercus* as the major arboreal taxa by 10,000 cal a BP (Fig. 3). A similar transition occurred at Butler Lake and throughout eastern Wisconsin with the present-day *Quercus-Ulmus-Fraxinus* forest developing around 8600 cal a BP (Long *et al*., 2011, Webb, 1987) (Fig. 3).

Fire history reconstruction

The charcoal records from each of the four sites exhibit somewhat individualistic patterns. Regional climate reconstructions indicate two periods of relatively cool and moist conditions: (1) 10,000 cal a BP to 8000 cal a BP, and (2) 5000 cal a BP to present time. The response to the higher overall effective moisture is generally seen at the two wetter sites as increased fire frequency and BCHAR influx throughout the middle and late Holocene. During the early Holocene wet period, Butler Lake fire frequency and BCHAR gradually increased, while Lake Seven fire frequency remained low and unchanged (Fig. 4). At the onset of the increased moisture conditions during the later Holocene (around 5000 cal a BP), Lake Seven BCHAR increased from .01 to .04 particles cm^{-2}, and fire episode frequency rose from 1 to 2 episodes per $1000a^{-1}$ (Fig. 4). However, Butler Lake BCHAR declined from .03 to .01 particles cm^{-2} at 5000 cal a BP, with fire episode frequency dropping from 2 to 1 events per $1000a^{-1}$ (Fig. 4). Thus, both BCHAR and fire frequency from Butler Lake and Lake Seven were sensitive to increasing moisture levels from 5000 cal a BP to present time, but responded differently (Fig. 4).

At the two dry locations—Comstock Lake and Lake George— there is little change in fire frequency and BCHAR values during the early Holocene, while peak magnitude at both locations slightly decreased throughout the early Holocene (Fig. 4). At Comstock Lake around 5000 cal a BP, BCHAR remains low (~.015 particles cm^{-2}) until present time. However, fire frequency increased from 1 to 6 events per $1000a^{-1}$ at 5000 cal a BP, decreased to 1 event per $1000a^{-1}$ at 2800 cal a BP, and then increased to 6 events per $1000a^{-1}$ near present time. A similar dramatic change in fire frequency from

1 to 6 events per $1000a^{-1}$ occurred at Lake George. BCHAR records, however, are similarly complacent at Lake George with a slow decrease from .07 to .02 particles cm^{-2} from 5000 to 3000 cal a BP (Fig. 4). Thus, these drier sites show little sensitivity in BCHAR during the regional increases in effective moisture. However, Lake George (5500 cal a BP) and Comstock Lake (5000 cal a BP) did show peaks in fire frequency, where moisture availability most likely provided abundant fuel loads, without oversaturation, for a brief period of short, intense forest fires to occur.

Fire episode synchronicity between sites

Fire episodes at the two sites with higher current precipitation as compared to paired current dry sites, demonstrate little to no synchrony at any time during the Holocene, despite a proximity of 5 km and overall similar vegetation type (Fig. 5). The CHAR records from Butler Lake and Seven Lake show independent fire episodes during the last 10,000 years. CHAR records from the two dry sites Comstock Lake and Lake George display synchrony at the 600-year time window (Fig 5).

Fire and fuel

All study sites showed unique fire-fuel relationships, however, some similarities are observed. All locations demonstrate periods of high BCHAR values and prominent fire intensity when the primary fuel sources were arboreal (ratio values nearer to 0), and during periods of low BCHAR values, the primary fuel sources were non-arboreal (ratio values nearer to 1.0) (Fig. 4).

Butler Lake fuel ratio values started high at 10,000 cal a BP at 1.0, indicating a high proportion of non-arboreal fuels. BCHAR values were low, ranging from 0 to 1 pieces cm^{-2}, and fire frequency ranged from 4 to 6 episodes per $1000a^{-1}$ (Fig. 4). Fuel ratios then decreased starting at c.8800 cal a BP, eventually reaching a low value of 0.1 at c.6500 cal a BP, indicating an increasing proportion of arboreal fuels, while BCHAR increased from 1 to 2 pieces cm^{-2}, and fire frequency remained at ~6 episodes per $1000a^{-1}$ (Fig. 4). The most dramatic change in the Butler Lake record after c.7000 cal a BP is a fluctuation in fire frequency between 4 and 7 episodes per $1000a^{-1}$. These significant fluctuations were not accompanied by changes fuel ratios. Fuel ratios then remained high ranging from ~0.3 to 0.6 from 6500 cal a BP to 1300 cal a BP, while BCHAR values increased, 1 to 4 pieces cm^{-2} at 5500 cal a BP, then dropping to 1, and fire frequency remained at 7 episodes per $1000a^{-1}$ at this time. Ratios continued to remain high (0.5), containing more non-arboreal fuels from c.1300 cal a BP to present time, while BCHAR values declined to 0.5 pieces cm^{-2}, and fire frequency dropped to 2 event per $1000a^{-1}$ (Fig. 4).

The other wet site, Lake Seven, demonstrated a similar range of absolute fuel ratio values during the Holocene, but a much different temporal pattern than Butler Lake. During the early Holocene (10,000 to 6500 cal a BP) Lake Seven fuel ratio values were low and gradually increased, indicating fewer non-arboreal fuels over the first 4500 years of the record. The ratio of non-arboreal to arboreal charcoal morphotypes increased from a value of 0.2 at 10,000 cal a BP to 0.6 at 6200 cal a BP (Fig. 4). During the early Holocene, BCHAR values were low while fire frequency steadily dropped (~ 1 pieces cm^{-2}; ~7 to 1 episodes per $1000a^{-1}$; Fig. 4). At 5200 cal a BP, fuel ratios decreased to 0.1, indicating more arboreal fuels, while BCHAR increased from 0.5 to 3 pieces cm^{-2}, and fire frequency was low at 2 episodes per $1000a^{-1}$ (Fig. 4). At 3200 cal a BP, fuel ratio values continued to increase, indicating more non-arboreal fuels, while BCHAR increased to 4 pieces cm^{-2}, and fire frequency decreased to 4 episodes per $1000a^{-1}$ (Fig. 4). At 1200 cal a BP, fuel ratios suddenly decreased and remained low, indicating more arboreal fuels, while BCHAR remained at 3 pieces cm^{-2}, and fire frequency remained at 4 episodes per $1000a^{-1}$ (Fig. 4).

Non-arboreal fuel sources also gradually became more dominant in the early-Holocene fires at Comstock Lake. The fuel source ratios decreased from 0.6 at c.10,000 cal a BP to 0.1 at c.7000 cal a BP, while BCHAR values remained consistently low at 1 to 2 pieces cm^{-2}, and fire frequency remained steady at ~5 episodes per $1000a^{-1}$ (Fig. 4). For the majority of the mid to late Holocene (7000 - 2000 cal a BP) fuel ratios remained low (0.1 to 0.2), indicating more arboreal fuels, while BCHAR values gradually increased from 1.5 to 2 pieces cm^{-2} (Fig. 4). At this time fire frequency increased from 5 to 10 episodes per $1000a^{-1}$ at c.3300 cal a BP (Fig. 4). Throughout the late Holocene (2000 - 1000 cal a

BP) fuel ratios rapidly increased from 0.3 to 0.75, containing more non-arboreal fuels, while BCHAR also increased from 2 to 3 pieces cm^{-2}, and fire frequency dropped to 5 episodes per $1000a^{-1}$ (Fig. 4). Fuel ratios then decreased to 0.3 near present time, while fire frequency dropped to 3 episodes per $1000a^{-1}$ near present time (Fig. 4).

Lake George fuel source ratios were low throughout the early Holocene (10,000 cal a BP to 4000 cal a BP) suggesting mostly arboreal fuels, before increasing after the mid Holocene, suggesting non-arboreal fuels, with little change in BCHAR influx (Fig. 4). At this time fire frequency shows an increase from 4 to 8 episodes per $1000a^{-1}$ (Fig. 4). From 4000 cal a BP to 1500 cal a BP, there was a period of low fuel ratios, suggesting a higher abundance of arboreal fuels, while fire frequency remained high from 8 to 10 episodes per $1000a^{-1}$ during this time (Fig. 4). Toward the late Holocene, fuel ratios then increased from 0.1 to 0.6, showing a higher abundance of non-arboreal fuels, for a period from 1500 cal a BP to 1000 cal a BP (Fig. 4). Arboreal fuels then decreased from 0.6 to 0.1 near 250 cal a BP and rose to 0.5 near present time, while fire frequency decreased from 10 to 5 episodes per $1000a^{-1}$ near present time (Fig. 4).

Discussion

Moisture availability influence on Holocene fire regimes

During a warming and wet early Holocene from 10,000 cal a BP to 8000 cal a BP, the retreat of the Laurentide Ice Sheet allowed moisture conditions to increase throughout the upper Midwest (Webb, 1987). Opposite responses are seen in fire frequency among the wet sites. This result does not provide support for our first hypothesis, that the fire regimes at sites with high modern MAP (Butler Lake and Lake Seven) would have responded similarly in the past to changes in moisture availability. Increases in fire frequency in the early Holocene at Butler Lake are likely due to lower moisture conditions directly surrounding the watershed, which would have likely promoted more frequent ignition rates of fuels, and for an increase in rate of spread when fires were occurring (Govender *et al.,* 2006). Decreases in fire frequency at Lake Seven could be due to relatively high moisture conditions as the larger marshlands surrounding the watershed, which would have increased saturation of local fuels, limiting ignition of fuels, and rate of spread (Govender *et al.,* 2006). Regional moisture increase seems not to have affected fire frequency at the drier locations.

Differential sensitivity to a change in moisture is also seen in the mid-Holocene dry period (8000 cal a BP to 5000 cal a BP), as fire frequency at Butler Lake remained high and constant, but slowly decreased at Lake Seven until an increase c.5000 cal a BP. Interestingly, the delayed response at Lake Seven can be attributed to the sustained high effective moisture throughout the watershed, as local marshlands maintained high water levels for much of the middle Holocene, while lake levels at Butler Lake likely decreased much more rapidly (Long *et al.* 2011). Increases in fire frequency and BCHAR values at dry locations directly follows the decrease in moisture levels throughout the region (Booth *et al.,* 2006), which would have been cause for more frequent non-stand replacing fires to occur and spread.

The overall pattern is one of idiosyncratic and site-specific response that is not consistent in time. It has been suggested that fire regime activity increases and decreases directly in response to climatic controls, such as changing temperatures on a global scale (Daniau *et al,* 2012). This is evident in our study locations, yet regional fire regimes throughout the Midwest are not collectively fluctuating in response to climatic controls in similar ways (Hotchkiss et al., 2007; Long et al., 2011). We see that there are site-specific mechanisms, such as local moisture conditions and fuel load saturation, that are creating unique fire-fuel relationships at each of these sites in southern Wisconsin. Forestry managers controlling fire in these mesic deciduous and oak-savanna forests would benefit from research that distinguishes fire regime characteristics on a site-based level.

Wet and dry site asynchronicity throughout the Holocene.

The fire history records of Butler Lake and Lake Seven display no periods of correlation throughout the past 10,000 years (Fig. 5). This is surprising considering their proximity, similar vegetation and climate histories. These results can be considered consistent with an overall driver of fire frequency by moisture, as asynchronicity between sites is likely due to differences in effective moisture (Long *et al.* 2011). The watershed of Butler Lake has unique topographic features that may have raised the water level in the surrounding marshes, producing and sustaining high effective moisture conditions. Lake Seven does not have these vast wetlands in its watershed; thus effective moisture at this site may respond more directly to periods of low moisture availability (drought). In addition, minor differences in slope can affect fuel conditions between sites. It has been previously suggested that site-specific differences between locations can strongly influence local fire regimes, in that regional climatic controls may be obscured by local controls such as: stochastic ignitions, topography, and fuel loads (Gavin *et al.,* 2006).

The two sites with drier modern climates, Comstock Lake and Lake George, display direct correlation at time step 600 from the K1D synchrony function, however there is no other evidence of direct synchrony throughout the remainder of the Holocene (Fig. 5). Again this is puzzling given the similarities between watersheds, as both are similar in relative area, and Lake George is only 1m deeper than Comstock Lake, which would not likely influence moisture conditions. Both locations also have similar topography, as they are both located on the southwestern edge of the Green Bay Lobe. However, these two locations are relatively far apart, 60 km, which is significant distance to cause site-specific moisture differentiation (Gavin *et al.,* 2006). Comstock Lake displayed higher sensitivity to low moisture conditions throughout the Mid-Holocene than Lake George, specifically the regional drought period at 4200 cal a BP.

The differences in charcoal morphotypes may reflect different available fuels due to vegetation structure at each site. Generally, Lake Seven and Butler Lake are both *Pinus* vegetation type during the early Holocene, yet arboreal fuels were dominant at Lake Seven and non-arboreal fuels were dominant at Butler Lake. Also, middle Holocene peaks in non-arboreal ratios at all four study sites coincide with the maximum expansion of prairie vegetation into southern Wisconsin centered around 6500 cal a BP. (Fig. 3). The vegetation fluctuations surrounding dry study sites are relatively gradual through time, and display some level of synchrony with changes in charcoal morphotypes throughout the majority of the Holocene. Yet, late Holocene fluctuations in charcoal morphotypes are not synchronous with any such changes in vegetation. Early Holocene morphotypes from the two dry sites indicate a gradual build-up of non-arboreal fuels that correlated with the establishment of *Quercus* vegetation into the region, from 9000 cal a BP to 6000 cal a BP (Figs. 3 and 4). Fuel morphotypes displayed little change throughout the mid Holocene from 6000 cal a BP to 3000 cal a BP (Fig. 4). From 3000 cal a BP to present both dry sites display high abundances of non-arboreal fuels, which shows no correlation with any major change in available fuel loads as seen in the pollen diagram from Comstock Lake (Figs. 3 and 4).

Fire intensity effects on available fuel type

There was support for our second hypothesis, that wet and dry sites showed an increase in arboreal fuel sources as fire activity increased. All four sites collectively display higher ratios of arboreal fuels burned during periods of high fire frequency. Similarly, during periods of relatively low fire activity, charcoal particles were composed of primarily non-arboreal sources (Fig. 4). This suggests that forest fires occurring during periods of low disturbance fire activity are likely not of high enough intensity to fully ignite arboreal sources and create more intensive fires, rather providing more opportunity for surface/ground fires to occur and deposit higher concentrations of non-arboreal charcoal pieces than that of arboreal sources (Jensen *et al.,* 2007). During periods high fire activity, the overall concentration of charcoal pieces is from arboreal fuel sources (Fig. 4). This suggests that during such times of high fire activity, fire episodes were properly fueled to promote high intensity that created larger and more intensive fires to occur, possibly crown fires such as those that occur in lodgepole pine (*Pinus contorta*) forests in the western U.S. (Turner and Romme, 1994).

Effect of vegetation on fire regime

Differences in fuel sources among the study sites throughout the Holocene is the most prominent observation from the records. Thus, there was support for our third hypothesis that vegetation composition at all sites was dynamic but was not the main factor in determining fire activity. For example, in the early Holocene (10,000 - 8600 cal a BP) Lake Seven had high concentrations of arboreal charcoal, while in contrast Butler Lake displayed high concentrations of non-arboreal fuels. These differences may be related to landscape-scale differences in vegetation type among sites, but generally a variety of fire regimes ranging from low-intensity frequent fires to high-intensity infrequent fires can be observed in modern *Pinus* and *Quercus* forests, the two dominant pollen taxa at all sites throughout most of the Holocene.

There are some changes in the pollen records that correspond with changes in charcoal morphotypes. The early Holocene non-arboreal fuels at Butler Lake can be linked with *Pinus* vegetation and the timing of regional *Pinus* forest establishment (Webb, 1987). Some species of *Pinus*, such as *P. resinosa*, are relatively tolerant of low-intensity ground fires (Habrouk *et al.,* 1999). Such fires do not produce high quantities of arboreal charcoal pieces, suggesting that understory shrubs and grasses are the dominant fuel source. Low-intensity fire regimes and high values of non-arboreal charcoal morphotypes may also reflect the mesic deciduous forests established later in the Holocene in this region. Pollen analysis indicates a dominant oak forest at several sites during the mid- to late Holocene. *Quercus* species possess thick bark that is highly fire-resistant and has low thermal conductivity (Abrams, 1992), thereby limiting the amount of arboreal fuel sources. Non-arboreal pollen types such as *Poaceae* and *Ambrosia* do not demonstrate regional synchrony, but these pollen types indicate the presence of herbaceous vegetation in which fires may be moisture-limited. Fuel limitation at times of high non-arboreal charcoal has also been interpreted in the African savanna biome from sediments of Lake Challa (Nelson *et al.,* 2012).

One remaining unsolved question is how the late-Holocene fire regimes at Comstock Lake and Lake George could have changed without any apparent change in the pollen assemblages. The amount of non-arboreal fuels started to increase at both sites starting at c.2000 cal a BP, yet there were no apparent synchronous changes in available fuels surrounding the watersheds as seen in the pollen diagram (Fig. 3). A slight increase in *Ambrosia* pollen may indicate an opening of the landscape during this time. It is possible that a structural change in oak forest, such as abundant understory fuel growth, allowed an increase in non-arboreal fuels throughout the late Holocene. Increased moisture has been shown to cause a build-up of deciduous herbaceous understory fuels in the tropical forests of Panama (Condit *et al.,* 1996).

Conclusions

The results from the paleoecological studies shown here provide valuable information about the predictability of fire regimes both regionally and globally. In particular, regional charcoal records demonstrate how such regimes may be governed from a single climatic driver such as temperature or precipitation (Daniau *et al,* 2012). We provide evidence for increased moisture availability result in both in increasing or decreasing fire return interval, due to interactions with fuel source (vegetation type) and fire intensity (crown fires v. surface fires). *Similar* regional analyses of fire frequency, as calculated from sedimentary charcoal, have demonstrated differences in fire regime among Alaskan tundra types—a biome previously thought to be homogenous with regard to fire (Kelly *et al.,* 2013). Regional differences among fire regimes in deciduous and coniferous forest types in North America certainly exist (Marlon *et al.,* 2009). Within a relatively similar physiographic area in southern Wisconsin, these site-specific patterns of fire history emphasize the need to accumulate a large number of charcoal records within a single region to capture the spatial and temporal heterogeneity of fire regimes.

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Figure 1. Location of four study sites in the state of Wisconsin, USA. Butler Lake and Lake Seven are the paired wet sites in the mesic deciduous forests. Comstock Lake and Lake George are the paired dry sites in the prairie oak savanna complex. Presettlement vegetation is from Robert W. Finley, modified by the Wisconsin Department of Natural Resources.

Figure 2. (a) Age verses depth model for Lake George, Wisconsin. (b) Age verses depth model for Comstock Lake, Wisconsin. Bars indicate 1 sigma radiocarbon ages from Table 1.

Figure 3. Pollen percentages for selected taxa from Butler Lake, Wisconsin, USA (A) and Comstock Lake, Wisconsin, USA (B) plotted against the age of the sediment core.

Figure 4. Sedimentary charcoal records from four sites in Wisconsin, USA. Butler Lake and Lake Seven have higher current MAP than Comstock Lake and Lake George. (A) Fire-episode frequency plotted as number of peaks ka^{1}. Boxes represent individual peak magnitude plotted as pieces cm^{2}. (B) Charcoal accumulation rates per time step (14 years for Lake Seven) with BCHAR, solid line, superimposed. Curves plotted against the calibrated age of the cores. (C) Ratio values of observed charcoal morphotypes quantified at each 1 cm interval. High values near 0.8 represent non-arboreal fuels as dominant morphotypes. Low values near 0 represent arboreal fuels as dominant morphotypes.

Figure 5. The bivariate K-function for testing synchrony over a range of temporal windows for (a) two modern wet sites, and (b) two modern dry sites. Two records were tested, where in the first a series of events are placed on random years and the second events are placed within 50 yr of those in the first record. The L-function (transform of the K-function) for the events in (a) with 95% confidence envelope (thin lines) based on 1000 randomizations. In (b) with 95% confidence envelope (thin lines) based on 1000 randomizations. (a) The function never exceeds the upper confidence envelope, indicating no correlation of event times within windows of that scale. (b) The function exceeds the upper confidence envelope at time step 600, indicating some correlation of event times within windows of that scale.

Table 1. Radiocarbon dates and calibrated ages for Lake George and Comstock Lake